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ON THE ORIGIN OF OATS

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INTRODUCTION

MAN has long been interested in the origin of his cultivated plants, for they are the foundations upon which his various civilizations have been built. Primitive peoples frequently regarded their plants as gifts of the gods, but modern man seeks more natural explanations, both to satisfy his curiosity and to provide a sound basis for plant improvement projects.

The present paper is an attempt to bring together the available evidence on the origin of oats, the world's fourth most important cereal crop (Stanton, 1953). It is proposed to attack the problem by reviewing: the several systems of classification of the genus *Avena* L., together with the geographical distributions of the species; the cytological and genetical interrelations; and finally, the impact of man upon the genus.

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PART I. CLASSIFICATION AND DISTRIBUTION

The genus *Avena* is generally considered as consisting

of two sections: *Euavena* Griseb., which contains the cultivated oats and related wild annuals; and *Avenastrum* C. Koch, which comprises about forty species of wild perennials, most frequent in northern Eurasia, but with two species native to western North America. By recent authors (Hitchcock, 1950; Clapham et al., 1952) the section *Avenastrum* is treated as the genus *Helictotrichon* Besser. In the present paper only the section *Euavena* will be considered.

Natural Systems of Classification

Three students, Cosson (1854), Thellung (1911) and Mal'tsev (1929), have each attempted to devise a natural classification for the section *Euavena*.

Cosson divided the section into subsection *Sativae* containing the cultivated species, and subsection *Agrestes* containing the wild. This division is based on the fact that the spikelets of the cultivated species are firmly attached to the rachilla and do not fall at maturity, whereas the spikelets of the wild species are articulated to the rachilla and fall spontaneously when ripe. Cosson further divided the *Agrestes* into the series *Biformes* in which only the lower floret is articulated so that the spikelet falls as a unit, and the series *Conformes* with all florets articulated and falling separately. The disposition of species by Cosson is:

Subsect. I. *Sativae*

A. sativa, *A. orientalis*, *A. strigosa*, *A. brevis*, *A. nuda*

Subsect. II. *Agrestes*

Series 1. *Biformes*

A. ventricosa, *A. sterilis*, *A. eriantha*

Series 2. *Conformes*

A. longiglumis, *A. clauda*, *A. hirsuta*, *A. fatua*

The system of Thellung is based on the assumption that each of the cultivated species is related to and derived from some wild species. Accordingly the *Sativae*

of Cosson are distributed between the *Biformes* and *Conformes*. Unfortunately several wild species are not considered. The disposition of species by Thellung is:

Subsect. I. *Biformes*

- A. sterilis* ssp. 1 *macrocarpa*
 ssp. 2 *byzantina*

Subsect. II. *Conformes*

- A. fatua* ssp. 1 *fatua*
 ssp. 2 *sativa* (incl. *A. orientalis*)
 ssp. 3 *nuda*
- A. strigosa* ssp. 1 *barbata*
 ssp. 2 *strigosa* (incl. *A. brevis*)
 ssp. 3 *Wiestii*
 ssp. 4 *abyssinica*

The system of Mal'tsev was developed after an extensive study of herbarium material and of a series of plantings of *Avena* species in various parts of the U.S.S.R. The material was gathered by the expeditions of Vavilov and associates, the geographical and ecological data collected by the expeditions being used in the treatment. On the basis of chromosome numbers Mal'tsev divided the section into subsection *Aristulatae* and subsection *Denticulatae*. Subsection *Aristulatae* contains the diploid and tetraploid species. It is regarded as the older, perhaps derived from section *Avenastrum*, with its center of origin in the western part of the Mediterranean region. Subsection *Denticulatae* contains the hexaploid oats and is believed to be the younger. It is regarded as having arisen from an unknown ancestral complex in the mountains of Central Asia, a conclusion which Schiemann (1932) says has not been shown to be based on fact. The characters used by Mal'tsev to define his subsections and series will be given in the key. In the following outline of the system all cultivated oats are marked by asterisks and each is believed to be derived from the wild subspecies which immediately precedes it. The division into

chromosome groups is provided for the convenience of the reader and is not part of Mal'tsev's system.

Subsection I. *Aristulatae*

Diploid Group $2n=14$

Series 1. *Inaequaliglumes*

1. *A. clauda*

2. *A. pilosa*

Series 2. *Stipitatae*

3. *A. longiglumis*

4. *A. ventricosa sens. ampl.*

ssp. 1. *ventricosa*

2. *Bruhnsiana*

Series 3. *Eubarbatae*

5. *A. strigosa sens. ampl.*

ssp. 1. *hirtula*

2. *strigosa**

Tetraploid Group $2n=28$

ssp. 3. *barbata*

4. *Wiestii*

5. *Vaviloviana*

6. *abyssinica**

Subsection II. *Denticulatae*

Hexaploid Group $2n=42$

6. *A. fatua sens. ampl.*

ssp. 1. *septentrionalis*

2. *nodipilosa**

3. *meridionalis*

4. *macrantha**

5. *fatua*

6. *sativa**

7. *cultiformis*

8. *praegravis**

7. *A. sterilis sens. ampl.*

ssp. 1. *Ludoviciana*

2. *pseudo-sativa**

3. *trichophylla*

4. *nodipubescens**

5. *macrocarpa*

6. *byzantina**

In the present paper, following Mordvinkina (1936), binomials are restored to several of the taxa treated as subspecies by Thellung and Mal'tsev. This is scarcely justifiable in the case of *A. strigosa sens. ampl.* which seems to form a unified although poorly understood group. The division of subsection *Denticulatae* into the traditional four species is also questionable, it being probable that these oats comprise but one highly polymorphous species. The present treatment follows common practice and is justifiable only for the sake of convenience.

Key for the Determination of Species

(largely after Mordvinkina, 1936)

- A. Lemma usually ending in two slender awns; plants mostly slender. (Subsect. *Aristulatae* Malz.)
 - B. Glumes very unequal, upper almost twice as long as lower; $2n=14$ (Series *Inaequaliglumes* Malz.)
 - C. All florets of spikelet articulated, falling separately at maturity *A. clauda*
 - C. Only lower floret articulated, spikelet falling as a unit *A. pilosa*
 - B. Glumes equal or subequal
 - D. Callus 5–10 mm. long, subulate; $2n=14$ (Series *Stipitatae* Malz.)
 - E. All florets articulated *A. longiglumis*
 - E. Only the lower floret articulated
 - F. Callus ± 5 mm. long; glumes 25–30 mm. long *A. ventricosa*
 - F. Callus to 10 mm. long; glumes to 40 mm. long *A. Bruhnsiana*
 - D. Callus about 2 mm. long; $2n=14$ or 28 (Series *Eubarbatae* Malz.)
 - G. Lemma ending in 2 awns and having 1 or 2 lateral teeth; glumes with 7–9 nerves
 - H. Lemma with 1 lateral tooth (sometimes none); awns at tip of lemma usually exerted beyond the glumes
 - I. Florets articulated, articulation-scar oblong-linear; awns at tip of lemma to 12 mm. long *A. hirtula*
 - I. Florets not articulated; awns 1–5 mm. long *A. strigosa*

- H. Lemma with 2 lateral teeth; awns not exerted
 - J. Florets articulated, scar oval or round
 - K. Awns at tip of lemma 3-6 mm. long *A. Wiestii*
 - K. Awns \pm 1 mm. long *A. Vaviloviana*
 - J. Florets not articulated; awns 1-4 mm. long *A. abyssinica*
 - G. Lemma ending in 2 awns to 5 mm. long, lateral teeth wanting; glumes with 9(10) nerves; articulation-scar oblong *A. barbata*
- A. Lemma usually ending in two small teeth, never produced into two setiform awns; plants mostly robust; $2n=42$ (Subsect. *Denticulatae* Malz.)
 - L. Lower floret articulated with the rachilla
 - M. Upper florets not articulated, spikelet falling as a unit *A. sterilis*
 - M. All florets articulated *A. fatua*
 - L. None of the florets articulated, separated by fracture of rachilla
 - N. Most of rachilla segment remains attached to upper floret on threshing; fracture surface at base of lower floret slanting *A. byzantina*
 - N. Rachilla segment remains attached to lower floret; fracture surface not slanting *A. sativa*

Distribution and Relationships of Avena Species

1. **A. clauda** Dur. A wild oat found in Algeria (Battandier and Trabut, 1904), Tripoli, Palestine (Post, 1933), Asia Minor, Iraq, Transcaucasia and eastward to Turkistan (Mal'tsev, 1929). Reported as rare in Attica, Greece (DeHalácsy, 1904).

Mal'tsev says this species more closely resembles the genus *Helictotrichon* than any other *Avena* species. He therefore considers it to be the most ancient, and to have given rise to the remainder of the *Aristulatae* through *A. longiglumis*.

2. **A. pilosa** M. Bieb. A wild oat occurring in northern Algeria (Battandier and Trabut, 1904), Tripoli, Syria (Post, 1933), Asia Minor, the Caucasus and eastward to southern Turkmenistan (Mal'tsev, 1929).

Battandier and Trabut, and Mordvinkina (1936) state that only the lower floret of *A. pilosa* is articulated, while Post (1933) says that none of the florets are jointed to the axis. Haussknecht (1894), according to Thellung (1911), noted the same variation and believed this species to be a variety of *A. clauda*, differing only in the manner of floret attachment. Mal'tsev treats *A. pilosa* as closely related to and derived from *A. clauda* by a side branch of the main phylogenetic trunk. Both species, according to him, have unequal glumes, a linear callus about 3 mm. long and a linear-elliptical articulation-scar.

3. ***A. longiglumis* Dur.** A wild oat found in southern Spain (Willkomm and Lange, 1870), Algeria (Battandier and Trabut, 1904), Palestine (Post, 1933) and Greece (DeHalácsy, 1904). Mal'tsev believes it to have given rise to *A. ventricosa* on the one hand, and to *A. strigosa sens. ampl.* on the other.

4. ***A. ventricosa* Bal.** A wild oat restricted to western Algeria (Battandier and Trabut, 1904; Mal'tsev, 1929). Mal'tsev derived this species from the preceding by a side branch of the main phylogenetic trunk. It resembles *A. longiglumis* in having equal glumes and a long callus with a narrow linear scar. It differs in having only the lower floret articulated, as in *A. pilosa*.

5. ***A. Bruhnsiana* Grun.** A wild oat restricted to the Apsheron Peninsula in eastern Transcaucasia, and treated by Mal'tsev as a subspecies of *A. ventricosa* from which it differs by the larger size of its spikelet-parts. Although the two are now separated by some 2500 miles, we do not know what migrations they may have undergone in the past. The wide gap is partially spanned by *A. longiglumis* from which they may have evolved independently.

6. *A. hirtula* Lag. = *A. strigosa* Schreb. ssp. *hirtula* (Lag.) Malz. A wild oat which is restricted to the western portion of the Iberian Peninsula (Mordvinkina, 1936). According to Thellung (1911) and Mal'tsev (1929), *A. hirtula* is intermediate in its characters between *A. Wiestii* and *A. barbata*. Mal'tsev derives the remaining diploid and tetraploid oats from this species.

7. *A. strigosa* Schreb. = *A. strigosa* Schreb. ssp. *strigosa* (Schreb.) Thell. The hairy or sand oat occurs as a weed throughout northwestern Europe from Portugal to southern Finland (Vavilov, 1926; Werth, 1944). Thellung reports it as sometimes cultivated on sandy soils in Portugal and Spain, western and central France, Belgium, northwestern Germany and Great Britain. Vavilov says it is only met with as a crop in France and Great Britain. In England it is rare and local, being found only as a weed in grain fields (Clapham et al., 1952), while Stanton (1936) reports that an improved strain has been developed in Wales. *A. strigosa* has two variants which are sometimes called species and sometimes proles (races). These are *A. brevis* and *A. nudibrevis*.

A. brevis Roth = ssp. *strigosa* prol. *brevis* (Roth) Hauskn. The short oat, like the typical *strigosa*, is adapted to unfavorable soil conditions and is sometimes cultivated in Portugal, Spain, France and northwestern Germany (Thellung, 1911). It is distinguished by its blunt lemmas which end in two teeth rather than in two awns.

A. nudibrevis Vav. = ssp. *strigosa* prol. *nuda* (L.) Hauskn. = *A. nuda* L. var. *biaristata* Asch. & Gr. The small-grained naked oat is occasionally cultivated in northwestern Germany (Vavilov, 1926). *A. nudibrevis* differs from the typical *strigosa* in having lemmas which do not become indurated at maturity, but remain membranous allowing the loosely enclosed grains to be readily threshed

free. It was once thought that all naked oats (the so-called species *A. nuda* L.) came from China where hexaploid naked oats are widely grown. The cytological work of Nikolaewa (1922) revealed that the small-grained naked oat was a diploid and undoubtedly European in origin. Later Mal'tsev showed *A. nuda* to be a highly diverse assemblage, containing, in addition to the present oat, four proles belonging to *A. sativa* and one to *A. byzantina*.

A. strigosa and its variants are the only diploid cultivated oats and are geographically isolated from all other diploids except *A. hirtula*. Mal'tsev derived *A. strigosa* from *A. hirtula*, a judgment sounder than those of Thellung (1911, 1928) and Trabut (1914) who suggested the tetraploid *A. barbata* had given rise to *A. strigosa*. De Candolle (1883) stated that *A. strigosa* appeared to be a form of *A. sativa*, so subtle are the differences between the various cultivated oats.

8. ***A. Wiestii* Steud.** = *A. strigosa* Schreb. ssp. *Wiestii* (Steud.) Thell. A desert plant which is widespread in North Africa (Trabut, 1914), Egypt (Täckholm et al., 1941), Syria and Palestine (Post, 1933), Iraq and rare in eastern Transcaucasia (Mal'tsev, 1929).

It is possible that both diploid and tetraploid oats exist which answer the description of *A. Wiestii*, but this will be considered later. Mal'tsev treats it as a tetraploid. Thellung (1911) and Trabut (1914) suggest that *A. Wiestii* is the wild species from which *A. abyssinica* has been derived, and in 1928 the former gave six transitional forms between the two.

9. ***A. Vaviloviana* (Malz.) Mordv.** = *A. strigosa* Schreb. ssp. *Vaviloviana* Malz. = ? ssp. *Wiestii* (Steud.) Thell. var. *pseudo-abyssinica* Thell. A wild oat restricted to Abyssinia and Eritrea (Mal'tsev, 1929).

A. Vaviloviana, which scarcely deserves the rank of species, appears to be a short-awned variety of *A. Wiestii*. It is regarded by Mal'tsev as the wild oat from which *A. abyssinica* has been derived.

10. ***A. abyssinica* Hochst. = *A. strigosa* Schreb. ssp. *abyssinica* (Hochst.) Thell. = *A. sativa* L. var. *abyssinica* Engler.** This oat is restricted to Abyssinia, Eritrea and Yemen (Mal'tsev, 1929) where it is both cultivated and semi-wild (Vavilov, 1926). Harlan reports (Stanton and Dorsey, 1927) observing it rarely in Abyssinia and only as an admixture in barley fields. The natives informed him they had seeded it in the barley fields intentionally.

A. abyssinica is the only cultivated tetraploid oat. It is described by Mal'tsev as having the awn-points at the tip of the lemma reduced to ± 1 mm. as in *A. Vaviloviana*. However, Stanton and Dorsey describe plants of this species as having the awn-points 2-4 mm. long. Evidently Mal'tsev was unaware of the range of variation in *A. abyssinica*.

11. ***A. barbata* Pott = *A. strigosa* Schreb. ssp. *barbata* (Pott) Thell.** A wild oat occurring along the Atlantic coast of Europe from Brittany southward, throughout the Mediterranean region (Thellung, 1911) and extending eastward through Transcaucasia and southern Turkistan to Afghanistan and the western Himalayas (Mal'tsev, 1929). *A. barbata* has been introduced into the United States, where it occurs as a common weed from Washington and Oregon to Arizona and California (Hitchcock, 1950).

12. ***A. sterilis* L. sens. ampl. excl. form. cult.** The wild red oat, a hexaploid complex distinguished by the lack of articulation of the upper florets, is an Old World species, ranging from the Atlantic to the Himalayas, and

may be divided into three subspecies: *sterilis*, *trichophylla* and *Ludoviciana*.

Ssp. *sterilis* = ssp. *macrocarpa* (Moench) Briq. A stout plant with large grains, spikelets with 3–5 florets, glumes 30–50 mm. long, culm-nodes glabrous. It is strictly Mediterranean in distribution (Mal'tsev, 1929).

Ssp. *trichophylla* (*C. Koch*) *Malz.* A more slender plant with medium-sized grains, spikelets with 2–3 florets, glumes 25–35 mm. long, culm-nodes pubescent. It shares the easternmost range of ssp. *sterilis* in Palestine, Syria and western Asia Minor, but it extends eastward through Asia Minor to Transcaucasia, western Iran and Iraq (Mal'tsev, 1929). Mal'tsev regards this subspecies as intermediate between ssp. *sterilis* and ssp. *Ludoviciana*.

Ssp. *Ludoviciana* (*Dur.*) *G. & M.*, is a plant with small grains, spikelets with 2 (rarely 3) florets, glumes 25–30 mm. long, and glabrous culm-nodes. It ranges from southern England (Clapham et al., 1952), through France, Switzerland, Italy (Thellung, 1911), Spain (Willkomm and Lange, 1870) to North Africa (Battandier and Trabut, 1904). It is scattered throughout the Mediterranean region and becomes more abundant from Asia Minor through southern Russia, the Caucasus, southern Turkmenistan and northern Iran to Afghanistan and Turkistan (Mal'tsev, 1929). This subspecies, which has the general aspect of *A. fatua*, occurs largely in areas where the ranges of *A. sterilis* and *A. fatua* meet or overlap.

Since the similarities between the two species were pointed out by Trabut (1914), it has been universally believed that *A. byzantina* has been derived from *A. sterilis*. Thellung (1928) has distinguished 15 transitional forms. Recently Coffman (1946) has proposed the theory that *A. sterilis* is the progenitor of all other hexaploid oats.

13. **A. byzantina** C. Koch, the cultivated red oat, is grown in southern Spain, southern Italy, Greece, North Africa and Asia Minor (Vavilov, 1926) and in the southern part of the United States, South America, Australia and New Zealand (Stanton, 1953).

A. byzantina, distinguished from *A. sterilis* by its non-articulate spikelets, has three subspecies: *byzantina*, *nodipubescens* and *pseudo-sativa*. According to Mal'tsev (1929), these are derived from *A. sterilis* subspecies *sterilis*, *trichophylla* and *Ludoviciana* respectively. Except for the non-articulate spikelets, the subspecies of *A. byzantina* resemble the subspecies of *A. sterilis* from which they are supposedly derived and may be determined accordingly.

Ssp. **byzantina**, the one most commonly cultivated, has the rare naked prol. *denudata* (Hausskn.) Malz. Ssp. **nodipubescens** Malz. occurs from Asia Minor to Palestine, while ssp. **pseudo-sativa** Thell. has been reported from Switzerland and Uruguay.

That *A. sterilis* has contributed to the formation of *A. byzantina* seems logical on the basis of geography and on the facts that both species are resistant to heat and cold and to many of the ordinary diseases of oats (Coffman, 1946). None of these similarities extends to *A. fatua*, the only other wild hexaploid oat. For the derivation of *A. byzantina* from *A. sterilis* it requires only that the spikelet-articulation of the latter cease to function. Vavilov (1950) placed the center of origin of *A. byzantina* in the Near East.

14. **A. fatua** L. sens. ampl. excl. form. cult. is a wild oat with a vast range across Eurasia from the Atlantic to Mongolia. It has been widely introduced into North America and is a troublesome weed in the hard spring wheat areas of Minnesota, the Dakotas, Montana and

adjacent Canada (Stanton, 1936). Thellung (1911) reports it to be adventive in South Africa, South America, Australia and New Zealand. Täckholm et al. (1941) report it from Egypt, Cyrenaica, Tunis, Algeria and Morocco. It may be divided into four subspecies: *meridionalis*, *septentrionalis*, *fatua* and *cultiformis*.

Ssp. ***meridionalis* Malz.**, with glumes to 30 mm. long, elongate-lanceolate lemmas to 25 mm. long and mostly glabrous culm-nodes, is the southernmost subspecies, ranging from the mountains of south central Asia through Afghanistan, Iran, Transcaucasia and Asia Minor to Egypt (Mal'tsev, 1929).

Ssp. ***septentrionalis* Malz.**, with glumes to 25 mm., lanceolate lemmas to 20 mm. long and culm-nodes always pubescent, extends from northern Russia and the Ural region through western and central Siberia to the Lake Baikal region and Mongolia, thence southwestward through the mountains of central Asia from the Altai to the Pamir Plateau, the Hindu Kush and the northwest Himalayas.

Ssp. ***fatua***, with glumes to 25 mm. long, lanceolate lemmas to 20 mm. long, grains 1.5–2 mm. thick, and culm-nodes always glabrous, is the western subspecies ranging from Turkistan and the Caucasus through southern Russia, Poland and the whole of western Europe.

Ssp. ***cultiformis* Malz.**, with glumes to 25 mm. long, ovate-lanceolate lemmas to 20 mm. long, grains 2–3 mm. thick, and with culm-nodes always glabrous, appears to have no well-defined geographical range. It is reported by Mal'tsev as being most common in North America, but occurring also in Europe eastward to central Russia.

A. fatua is generally believed (Thellung, 1911; Traut, 1914; Mal'tsev, 1929) to be the progenitor of *A. sativa* and Thellung (1928) gave 21 transitional forms. It will be recalled that Thellung (1911) placed *A. sterilis*

and its derivatives in subsection *Biformes* and *A. fatua* with its derivatives in subsection *Conformes*. Similarly Mal'tsev divided the hexaploid oats into two independent species: *A. fatua sens. ampl.* and *A. sterilis sens. ampl.* Coffman (1946), however, is convinced that all hexaploid oats are derived monophyletically from *A. sterilis*, and regards *A. fatua* as an aberrant weed. It must be remembered, however, that it is the cultivated oats, with their lack of floret-articulation, which are "aberrant." *A. fatua*, although a weed, is a perfectly normal self-propagating grass.

15. **A. sativa L.**, the common cultivated oat, is widely grown throughout northern Eurasia and in the northern United States and Canada. According to Stanton (1953), it is the most important cultivated oat.

A. sativa may be divided into four subspecies: *macrantha*, *nodipilosa*, *sativa* and *praegravis*, derived according to Mal'tsev (1929), from subspecies *meridionalis*, *septentrionalis*, *fatua* and *cultiformis* of *A. fatua* respectively. Except for the non-articulate florets, the subspecies of *A. sativa* resemble the subspecies of *A. fatua* from which they are supposedly derived and may thus be determined.

Ssp. **macrantha** (*Hack.*) *Malz.* occurs as a weed in grain fields over much of the same range as *A. fatua* ssp. *meridionalis*. It has the rare naked prol. *nudata* *Malz.*

Ssp. **nodipilosa** *Malz.* is cultivated principally in northern Russia, the Ural region, Siberia and Mongolia. It has the naked prol. *decorticata* *Malz.* which is cultivated in Mongolia and northern China.

Ssp. **sativa** is the most commonly cultivated oat. It has the naked prol. *chinensis* (*Fisch.*) *Malz.* which is sometimes grown in Europe and North America.

Ssp. **praegravis** (*Krause*) *Malz.* is cultivated principally in southern Russia, Europe and North America.

Its naked prol. *grandiuscula* Malz. is sometimes grown in Europe and North America.

The so-called *A. orientalis* Schreber is any form of *A. sativa* with a condensed, one-sided panicle, a not infrequent variation.

The similarity between the ranges of *A. fatua* and *A. sativa*, which extends to the subspecies, suggests a close relationship between the two, as does the parallel variation of the subspecies. The morphology of the spikelets of the two species also suggests a relationship, for with *A. sativa*, when the upper florets are separated by fracture of the rachilla, the rachilla segment remains attached to the lower floret exactly as with *A. fatua*, and different from *A. sterilis* and *A. byzantina* where the rachilla segment remains attached to the upper floret. These similarities have previously been interpreted as indicating that *A. sativa* arose from *A. fatua*, but Coffman (1946) has suggested the reverse might be true. Vavilov (1950) placed the center of origin of *A. sativa* in the Near East region.

Conclusions

From the foregoing discussion it seems clear that the diploid species, with the notable exception of *A. strigosa*, have limited ranges in the Mediterranean region, a few also extending into the Near East. The tetraploids occupy the same general area as the diploids, but are better represented in the Near East. *A. Vaviloviana* and *A. abyssinica*, however, are somewhat isolated to the south. The hexaploids *A. sterilis* and *A. byzantina* are largely restricted to the Mediterranean and Near East regions, while *A. fatua* and *A. sativa* extend from those regions far to the north and northeast.

It is also clear that phylogenetic studies have reached an unanimous conclusion on the derivation of the cultivated species only in the case of *A. byzantina*. The interrelationships among the wild species are equally obscure.

PART II. THE EVIDENCE FROM CYTOLOGY

Chromosome Numbers

Following is a list of the chromosome numbers which have been reported for *Avena* species, together with authorities for the counts. The list of authorities is incomplete, but in cases of disputed counts it indicates which count has been verified by several authors.

1. <i>A. clauda</i>	2n=14	Nikolaewa, 1922; Emme, 1930.
2. <i>A. pilosa</i>	2n=14	Nikolaewa, 1922.
3. <i>A. longiglumis</i>	2n=14	Ellison, 1940.
4. <i>A. ventricosa</i>	2n=14	Emme, 1930.
5. <i>A. Bruhnsiana</i>	2n=14	Emme, 1930.
6. <i>A. hirtula</i>	2n=14	Emme, 1930; Ellison, 1940.
7. <i>A. strigosa</i>	2n=14	Kihara, 1919; Nikolaewa, 1922; Winge, 1925; Aase and Powers, 1926; Huskins, 1927; Nishiyama, 1929; Emme, 1930; Spier, 1934; Ellison, 1940.
8. <i>A. Wiestii</i>	2n=14	Dorsey, 1925; Aase and Powers, 1926; Huskins, 1927; Kihara and Nishiyama, 1932; Spier, 1934; Ellison, 1940.
	2n=28	Emme, 1930.
9. <i>A. Vaviloviana</i>	2n=28	Emme, 1930.
10. <i>A. abyssinica</i>	2n=28	Stanton and Dorsey, 1927; Emme, 1930; Kihara and Nishiyama, 1932; Spier, 1934; Ellison, 1940.
11. <i>A. barbata</i>	2n=28	Kihara, 1919; Dorsey, 1925; Huskins, 1927; Nishiyama, 1929; Emme, 1930; Spier, 1934; Ellison, 1940.
	2n=32	Nikolaewa, 1922.
12. <i>A. sterilis</i>	2n=42	Kihara, 1919; Huskins, 1927; Nishiyama, 1929; Emme, 1930; Spier, 1934.
	2n=44	Nikolaewa, 1922.
13. <i>A. byzantina</i>	2n=42	Kihara, 1919; Dorsey, 1925; Huskins, 1927; Nishiyama, 1929; Emme, 1930.
	2n=44	Nikolaewa, 1922.
14. <i>A. fatua</i>	2n=42	Kihara, 1919; Huskins, 1927; Nishiyama, 1929; Emme, 1930.
	2n=48	Nikolaewa, 1922.
15. <i>A. sativa</i>	2n=42	Kihara, 1919; Winge, 1926; Aase and Powers, 1926; Huskins, 1927; Nishiyama, 1929; Emme, 1930; Spier, 1934.
	2n=48	Nikolaewa, 1922.

The counts obtained by Nikolaewa on the polyploid species differ from those of all other workers and probably represent errors.

The case of *A. Wiestii* is a different matter. Emme (1930), working in conjunction with the taxonomist Mal'tsev, found *A. Wiestii* to be a tetraploid, but stated that an oat from Palestine, which Vavilov said was essentially *A. Wiestii*, was a diploid. The oat found by Spier (1934), Huskins (1927) and Dorsey (1925) to be diploid is described by Stanton and Dorsey (1927) and is said to have been received from Egypt. It also appears to be essentially *A. Wiestii* except for usually having 9-nerved glumes. *A. Wiestii sensu* Mal'tsev has glumes with 7(8) nerves. Similarly *A. barbata* may have both diploid and tetraploid forms. Jones (1940) reports having received many years ago, as an impurity in seed of *A. Wiestii*, an oat which was identified as *A. barbata* until Ellison (1938) found it to be a diploid. This diploid oat goes under the designation of Cc1795. Clearly more work is required before the relationships between the diploid and tetraploid species can be understood.

Genome Analysis

Although the chromosome numbers indicate certain *Avena* species to be polyploids, every cytologist and geneticist who has studied the polyploid species has found them to behave like diploids with complete bivalent formation at meiosis and high fertility. In discussing how this situation came about, Philp (1933) suggested the tetraploids may be auto- or allopolyploids arising from one or two diploid species, while the hexaploids probably arose from a tetraploid and a diploid and so ultimately may have been derived from two or three diploid species. The study of chromosome pairing at meiosis in the F₁ hybrids of interspecific *Avena* crosses has shed a certain

amount of light on the origins of the polyploid species, as well as the relationships between species having the same chromosome number.

Diploid \times *Diploid*—Genome analyses between diploid *Avena* species have been restricted to the series *Eubarbatae*. The F_1 of *A. strigosa brevis* \times *A. strigosa* showed normal bivalent formation (Ellison, 1938). The chromosomes of *A. Wiestii* are very similar to those of *A. strigosa*, as Nishiyama (1933) crossed these two species with a synthetic diploid and 7 normal bivalents were observed in the F_1 of both crosses.

The chromosomes of *A. hirtula* show slight structural differentiation from those of *A. strigosa*, for in the F_1 of *A. hirtula* \times *A. strigosa brevis* Ellison (1940) found complete pairing in most cells, but 1% of the cells examined showed 6 bivalents and 2 univalents while in many cells 1 bivalent was found to consist of heteromorphic homologues. Greater differentiation is shown by the oat Cc1795 which has been crossed with *A. Wiestii* and *A. strigosa brevis* (Ellison, 1940), and in both cases 5 bivalents and 1 quadrivalent were regularly observed.

The above evidence suggests the chromosomes of *A. strigosa*, *A. Wiestii* and the synthetic diploid are very similar. Nishiyama (1936) has represented the genome of these species as AA. Although showing some differentiation, the genome constitution of *A. hirtula* and Cc1795 appears to be AA also.

Tetraploid \times *Tetraploid*—Ellison (1938) observed meiotic behavior in the F_1 of *A. barbata* \times *A. abyssinica* and found complete bivalent formation in most cells. However, 15% of the cells showed 1 quadrivalent and cells having no quadrivalent sometimes had 2 or 4 univalents or a univalent and a trivalent. Ellison believed this irreg-

ularity to be due to segmental interchange. Otherwise the genome constitution of *A. barbata*, which was represented as AAB'B' by Nishiyama (1936), seems identical to that of *A. abyssinica*.

Hexaploid × *Hexaploid*—Nishiyama (1929) examined chromosome pairing in the F₁ of four hexaploid species combinations and found 21 normal bivalents in the majority of cells. Sometimes, however, 1 or 2 bivalents failed to form properly, resulting in univalents, a trivalent or a quadrivalent. Nishiyama suggested these irregularities were probably caused by mating between semi-homologous chromosomes which are not normal partners. Nishiyama expressed the degree of affinity between the genomes of the various species by the ratio of the number of bivalents found in the F₁ to the number expected. Full affinity between the parental genomes was given the value of unity, while no affinity was equal to zero. The values obtained by Nishiyama are:

<i>A. fatua</i>	0.998	<i>A. sativa</i>
<i>A. fatua</i>	0.992	<i>A. sterilis</i>
<i>A. sativa</i>	0.983	<i>A. byzantina</i>
<i>A. sterilis</i>	0.986	<i>A. byzantina</i>

Spier (1934) reported complete bivalent formation in the F₁ of *A. sterilis* × *A. sativa*. A few cells damaged by pressure showed two univalents.

Joshi (1951) studied meiotic behavior in the F₁'s of crosses involving *A. sativa*, *A. sterilis* and *A. fatua* and found 6–13% of the pollen mother cells showed irregularities, the nature of which was not stated. The parental species showed less than 2% irregularity, while the F₁ of spring × winter varieties of *A. sativa* showed 14–31% of the cells having irregularities. In hybrids of *A. byzantina* with *A. sterilis*, *A. sativa* and *A. fatua* 59–88% of the cells showed irregularities. These results are prob-

ably comparable to those of Nishiyama (1929) who, in hybrids involving *A. byzantina* as one parent, found univalents in 29–33% of the cells examined, while in hybrids involving only *A. sativa*, *A. sterilis* and *A. fatua*, univalents were found in 5–16% of the cells.

From the above evidence it is clear that a high degree of homology exists between the genomes of the various hexaploid species. Nishiyama (1939) gave AABBCC as the genome constitution of *A. fatua* and it is probable that this applies to all the hexaploid species.

Tetraploid × *Diploid*—Meiosis in the triploid F_1 of *A. barbata* × *A. strigosa* was investigated by Nishiyama (1929) who found the close genome affinity of 1.041 between the two species. Usually 7 bivalents inclusive of trivalents were formed, but sometimes 8–9 bivalents inclusive of trivalents were found. The number of trivalents was 0–3 and rarely a quadrivalent was seen. However, at least 3 lagging univalents were found at metaphase I of all cells. Spier (1934) made the same cross and reported similar results, except that at least 4 univalents were found in all cells.

Nishiyama (1936) made a further study of the genome constitution of *A. barbata* by crossing it with a synthetic autotetraploid of *A. strigosa* having the genome constitution of AAAA. In the F_1 hybrid 12 bivalents were frequently found and sometimes 13. The number of univalents found varied from 0 to 5, but in most cases was 1 or 2. In an extreme case all chromosomes entered into pairing relations, forming 11 bivalents and 2 trivalents. Thus it is evident that one genome of *A. barbata* is completely homologous with genome A of *A. strigosa*, while the second is partially homologous to it. Nishiyama represented the genome constitution of *A. barbata* as AAB'B'.

Ellison (1940) reported the meiotic behavior of the triploid F_1 of *A. longiglumis* \times *A. abyssinica*. The most frequent configuration found in 45% of the cells examined consisted of 5 univalents, 5 bivalents and 2 trivalents. Quadrivalents were rare, but each cell showed at least 1 trivalent or 1 quadrivalent. One cell had 4 univalents, 5 bivalents, 1 trivalent and 1 quadrivalent. As the meiotic behavior of this hybrid is very similar to that of *A. barbata* \times *A. strigosa* and because the pairing in the F_1 of *A. barbata* \times *A. abyssinica*, as discussed above, is very close, it seems certain that the genome constitution of *A. abyssinica* is AAB'B'. However, it is not clear whether *A. longiglumis* is AA or B'B'.

Hexaploid \times *Diploid*—The meiotic behavior of the tetraploid F_1 of *A. sativa* \times *A. strigosa* was reported by Kihara and Nishiyama (1932). The number of bivalents expected would be 7, while the number found ranged from 3 to 9 with the mode being 7. Multivalents found in the majority of cells had from 3 to 7 members. The same workers reported that in the tetraploid F_1 of *A. fatua* \times *A. strigosa* the situation was similar, but with the pairing perhaps a little weaker. The number of bivalents ranged from 2 to 9 with the mode being 6. Among the multivalents one eight-membered structure was found. The multivalents were believed to be formed by the supernumerary chromosomes of *A. sativa* and *A. fatua* pairing among themselves. As it is impossible to tell how many bivalents are formed in this way, it cannot be considered as demonstrated that *A. strigosa*, *A. sativa* and *A. fatua* have a common genome.

On the other hand, Ellison (1940) reported that in the tetraploid F_1 of *A. longiglumis* \times *A. sativa* there were usually at least 7 bivalents in each cell. Trivalent and quadrivalent formation were found to be less common

than in the triploid *A. longiglumis* \times *A. abyssinica*. Thus it is possible that one genome of *A. sativa* is homologous to the genome of *A. longiglumis*, but we do not know whether the genome of *A. longiglumis* is A or B'.

Hexaploid \times *Tetraploid*—Nishiyama (1929) studied pairing behavior in the F_1 pentaploid hybrids of *A. barbata* \times *A. fatua* and *A. barbata* \times *A. sterilis*. Chromosome pairing was generally found to be loose with the bivalents formed often mated only at one end. On the basis of full homology 14 bivalents would be expected, but in *A. barbata* \times *A. fatua* 2–11 bivalents inclusive of 1–4 trivalents were found, while in *A. barbata* \times *A. sterilis* 7–13 bivalents inclusive of 0–4 trivalents were found. The genome affinity between *A. barbata* and *A. fatua* was 0.456 and between *A. barbata* and *A. sterilis* it was 0.675. These figures are even more significant when it is recalled that the chromosomes of *A. barbata* can pair among themselves as can the chromosomes of the hexaploids.

Emme (1932) reported that meiosis in the F_1 of the two pentaploid hybrids *A. sativa* \times *A. abyssinica* and *A. sativa* \times *A. barbata* showed 7 to 9 bivalents. Similarly Spier (1934) reported that meiosis in the F_1 of *A. abyssinica* \times *A. sterilis* showed 5 to 11 bivalents with 23 to 13 univalents per cell. Trivalents were sometimes found but not quadrivalents. These results agree with those of Nishiyama in indicating a very low homology between the genomes of the tetraploid and hexaploid species studied.

The lack of homology between the genomes of the tetraploids and hexaploids was further demonstrated by Lesik (1948) who obtained synthetic amphidiploids of *A. sativa* \times *A. abyssinica* using colchicine. These plants had 35 pairs of chromosomes and 100% fertility. Ex-

amination of meiosis showed 35 bivalents were usually formed, but sometimes 2-3 univalents were observed.

Conclusions

The evidence from cytology indicates that speciation on the diploid level in *Avena* has involved structural changes in the chromosomes, but these changes have not been extensive in the species so far investigated. Our ignorance of the genome constitution of many of the diploid species is complete.

The evidence indicates that the tetraploid *Avena* species have two partially homologous genomes which are also homologous to the genomes of the diploid species investigated. Whether the tetraploids are auto- or allopolyploids is not clear. Evidence on this point could readily be obtained by synthesizing tetraploids involving the various diploid combinations. The tetraploid species may have arisen independently or they may be derived from a common tetraploid ancestor.

The origin of the hexaploid species is obscure. While it is probable that at least one diploid *Avena* genome is present in the hexaploids, it is certain that *A. barbata* and *A. abyssinica* played no part. The identity of the tetraploid which did contribute two genomes to the hexaploids is a complete mystery. As with the tetraploids, the evidence from cytology does not indicate whether the hexaploids arose independently by allopolyploidy or whether the different species are derived from a common hexaploid ancestor or whether a combination of these processes has occurred.

PART III. THE EVIDENCE FROM GENETICS

Studies on the inheritance of taxonomic characters in the genus *Avena* have been largely restricted to the manner of attachment of the florets to the rachilla. The culti-

vated species of oats are distinguished from their supposed wild ancestors by the absence of floret-articulation. This distinction is not only important taxonomically, but economically, as it facilitates harvesting the grain, and biologically, as it deprives the cultivated species of self-propagating ability and makes them dependent upon man for continued existence. The modes of inheritance of the floret-attachment type of the cultivated oats afford valuable criteria for evaluating the various theories on the origin of the cultivated species.

Diploid and Tetraploid Species

Jones (1940) made a study of the mode of inheritance of the floret-attachment types of diploid and tetraploid species. Four diploid crosses were made: *A. Wiestii* (wild) \times *A. strigosa brevis* (cult.); *A. Wiestii* \times *A. strigosa*; *A. hirtula* (wild) \times *A. strigosa brevis* and Cc1795 (wild) \times *A. strigosa brevis*. In each cross all individuals of the F_1 had the florets articulated, while the F_2 segregation indicated the lack of articulation of the cultivated species to be due to two pairs of recessive factors. The genotype of the wild species for these factors was given as XXYY and that of *A. strigosa* as xxyy.

In the tetraploid cross *A. barbata* (wild) \times *A. abyssinica* (cult.) Jones found the F_1 to have all florets articulated, while the F_2 segregation indicated the solid floret-attachment of *A. abyssinica* to be due to four pairs of recessive factors. The genotype of *A. barbata* was given as XXXXYYYY and that of *A. abyssinica* as xxxxyyyy. Emme (1934) reported that in the F_1 of *A. abyssinica* \times *A. Vaviloviana* the wild-type attachment of the latter dominated. The F_2 segregation was not given.

The sterile triploid F_1 of *A. barbata* \times *A. strigosa* had the wild-type articulation (Nishiyama, 1929) as did the triploid F_1 of *A. longiglumis* \times *A. abyssinica* (Jones, 1940).

Thus it appears that the cultivated diploid and tetraploid oats arose from their wild ancestors by recessive mutation. The geographic isolation of both species from the main populations of the wild diploid and tetraploid species has undoubtedly been an important factor in the evolution of these oats.

Avena sativa

The common cultivated oat is generally believed to have arisen from *A. fatua*. In addition to its lack of floret-articulation, the cultivated species is distinguished from its putative ancestor by lacking prominent hairs about the base of the lemma and by having greatly reduced dorsal awns. The inheritance of these characters in crosses between the two species has been investigated by many workers (see Huskins, 1946) and the combination of characters behaves genetically as if due to a single gene or gene complex. The F_1 is intermediate between the two parents in having a twisted geniculate awn only on the lower floret, while the pubescence and articulation-surface are much reduced compared to *A. fatua*. The F_2 segregates in the ratio 1 *sativa*-like : 2 intermediate : 1 *fatua*-like for these characters.

Considerable light has been shed on the nature of the genetic factor governing the distinction between these two species by the study of fatuoids or false wild oats. This problem has been extensively reviewed by Huskins (1946), so only the barest outlines will be presented here. Fatuoids are derivatives or "off types" of *A. sativa* which arise spontaneously in many varieties of the cultivated oats and resemble *A. fatua* in type of floret-articulation, grain-pubescence and awn-development, but resemble the variety from which they arose in all other characters. Huskins presents convincing evidence that fatuoids are caused by chromosome aberrations which give rise to

plants deficient for the factor expressing the cultivated-type grain characters. Sometimes the fatuoids lack the entire chromosome which carries this factor. It is evident that *A. sativa* has all the genetic factors necessary to produce the *A. fatua* grain characters, but in addition it has a partially dominant inhibitor which suppresses the development of the *fatua* grain characters and produces the cultivated-type grain. This inhibitor is designated the C-factor and the chromosome on which it is located is called the C-chromosome.

The C-factor of *A. sativa* has been found to be partially dominant in crosses with wild species other than *A. fatua*. Florell (1931) reported that in crosses of *A. sativa* \times *A. sterilis* the *sativa*-type attachment of the lower floret (spikelet) was almost completely dominant over the wild type and due to a single factor. Jones (1940) found the F_1 of the crosses *A. longiglumis* \times *A. sativa* and *A. sativa* \times *A. barbata* to have non-articulate florets.

Theories accounting for the origin of *A. sativa* must agree with the genetic facts. Since the *sativa* grain type is due to a single factor pair, only one intermediate form is possible between the wild and cultivated grain types. This would be due to the heterozygous condition. An extensive series of intermediate forms from the wild species to *A. sativa* showing gradual reduction of the articulation-surface of the florets, reduction in pubescence, or reduction of awns has nothing to do with the origin of *A. sativa*. Far from solving the problem, such intermediate forms raise the additional question of their own origin. Similarly the facts of genetics are at variance with the opinion of Coffman (1946) that an origin of *A. sativa* from *A. sterilis* requires only loss mutations, while an *A. fatua* derivation requires additive mutations which are believed to be more difficult to obtain. The evidence indicates that both *A. sterilis* and *A. fatua* lack the C-

factor, and the derivation of *A. sativa* from either would require an additive mutation.

Avena sterilis

The wild red oat is distinguished by having the lower floret of a spikelet articulated, while the upper florets are not. When the upper florets are separated by fracturing the rachilla, most of the rachilla segment remains attached to the floret above. This character was used by Cosson as the basis of his series *Biformes*.

Like the C-factor of *A. sativa*, genetical studies have shown this *Biformes* character to be due to a single dominant gene, here called the B-factor. 'Tschermak (1929) reported that in the F₁ hybrids of *A. fatua* × *A. sterilis* the B-factor was completely dominant and the segregation of later generations showed it to be due to a unit factor difference. Similarly Florell (1931) reported that in various crosses of *A. sterilis* with *A. fatua* the B-factor was dominant in the F₁, while the F₂ segregated in the ratio of 3 *sterilis*-like : 1 *fatua*-like for this character.

Florell also crossed *A. sterilis* with *A. sativa* and found the F₁ plants to have non-articulate lower florets (spikelets) as in *A. sativa*, as well as non-articulate upper florets as in both parents. However, when the upper florets were separated by fracture, the rachilla segment remained with the floret above as in *A. sterilis*. The F₂'s segregated in the ratio of 1 *sativa*-like : 2 intermediate, like the F₁ : 1 *sterilis*-like, indicating linkage for the B- and C-factors. No cross-over plants were found.

Nishiyama (1935) obtained further evidence on the nature of the B-factor by crossing *A. sterilis* with a heterozygous fatuoid from *A. sativa* having only one C-chromosome. Plants were obtained in the F₂ which had 40 chromosomes, thus lacking the C-chromosome entirely. Such plants were fatuoids having the grain char-

acters of *A. fatua*. Thus it was demonstrated that the B-factor is carried on the C-chromosome. Whether or not the B-factor is an inhibitor of the *A. fatua*-type of upper floret-articulation is unknown, as fatuoids have not been observed in *A. sterilis*.

A. sterilis has the distinction of being the only hexaploid species which has not been theoretically derived from some other hexaploid *Avena* species now living. If it arose independently by allopolyploidy, one can scarcely resist suggesting *A. Bruhnsiana*, with its large spikelets and non-articulated upper florets, as the diploid ancestor.

Avena byzantina

The nature of the genetic mechanism controlling the grain characters of the cultivated red oat is by no means clear. Some forms of this species seem to have both the B- and C-factors on the same chromosome. This is true of cultivar Fulghum which Florell (1931) crossed with *A. fatua*. The F_2 segregated in the ratio of 3 *byzantina*-like to 1 *fatua*-like for the grain characters. Among the 478 plants of the F_2 were 4 cross-over progeny resembling *A. sterilis* and 3 resembling *A. sativa*. Stanton et al. (1926) found fatuoids arising from Fulghum and Burt to resemble *A. fatua*, indicating that the B- and C-factors were inhibiting the development of wild-type genes possessed by those varieties.

A. byzantina cultivar Coastblack, however, seems to have the B- and C-factors on the same chromosome, as well as an additional B-factor on another chromosome. In the cross Coastblack \times *A. fatua* Florell (1931) obtained an F_2 ratio of 12 *byzantina*-like : 3 *sterilis*-like : 1 *fatua*-like for the grain characters.

Bond, which is said to belong to *A. byzantina*, has no C-factor at all, but has the B-factor, as is shown by the work of Hayes et al. (1939), Torrie (1939) and Ko

et al. (1946). The spikelets of Bond shatter readily.

Coffman et al. (1925) made an extensive study of variability in *A. byzantina* cultivar Burt and found a most confusing array of forms. Some plants had the lower floret (spikelet) articulated while others did not. In some plants the rachilla segment when fractured remained with the floret above, in others it remained with the floret below, while in still others it fractured near the middle, parts remaining with both florets.

Mal'tsev (1929) and Mordvinkina (1936) state that all the florets of *A. byzantina* are non-articulate, while the latter author is able to distinguish between the grains of *A. sativa* and *A. byzantina* by the angle of the fracture-surface of the lower florets. If his *A. byzantina* has the C-factor, the difference between it and *A. sativa* might be due to the C-factor being superimposed on the different genetic backgrounds of the two species. The alternative is that non-articulate florets in many varieties of *A. byzantina* are due to other genetic factors than the C-factor. Clearly more information is needed before definite conclusions can be drawn.

Avena fatua

The genetic evidence indicates that the factors governing complete floret-articulation of the wild oats are inhibited by the B- and C-factors. It is sometimes assumed that the articulation factors of *A. fatua* are located on a single chromosome which is called the B-chromosome. There is no evidence for this, it being probable that many factors on many chromosomes are responsible for the grain characters of *A. fatua*.

It is generally believed that *A. fatua* is the progenitor of *A. sativa* and, as stated earlier, their parallel variation and geographic distribution speak for a close relationship between the two. However, no one has observed any

strain of *A. fatua* to mutate to *A. sativa*. Vavilov (1926) noted that no attempt to cultivate *A. fatua* would induce it to lose its brittle manner of floret-attachment. Coffman (1946), stated that, despite the fact that *A. fatua* is a common weed of fields and fence rows in the western United States, there is no evidence of any cultivated form having arisen from it.

On the other hand, both *A. byzantina* and *A. sativa* have given rise to fatuoids resembling *A. fatua*, and Coffman (1946) stated that he was inclined to believe the origin of *A. fatua* paralleled that of the fatuoids. Earlier (1936) Stanton wrote: "To one with imagination, the occurrence of fatuoids might be considered a provision of nature to return cultivated oats to wild forms, thus making them self-propagating in case, through some disaster, the cultivated forms were no longer in the hands of human beings."

If it is true that *A. fatua* arose from cultivated oats and if all cultivated oats arose from *A. sterilis* and if the cultivated oats are not self-propagating, then *A. byzantina*, *A. sativa* and *A. fatua*, including a total of eleven subspecies, have evolved within the period of man's agricultural activities. This would be exceedingly explosive evolution.

Conclusions

The evidence from genetics indicates that the lack of floret-articulation of the diploid and tetraploid cultivated oats is due to different genetic factors than the similar character of the hexaploid cultivated species. It may be concluded that different evolutionary forces have produced similar results in the two subsections. Although it seems probable that recessive mutations and geographic isolation have produced the diploid and tetraploid cultivated species, the mode of origin of the hexaploid cultivated oats is by no means clear. The final decision on

the origin of the hexaploid species will have to await the discovery of their tetraploid ancestor(s).

Much work remains to be done in determining the genetic mechanism controlling taxonomic characters other than floret-attachment type. Such studies may provide critical information for evaluating Mal'tsev's system of classification. Indeed, it is now known that the B-factor controls the distinction between *A. sterilis sens. ampl.* and *A. fatua sens. ampl.* Species based on a single gene difference may not be too valid.

PART IV. OATS AND MAN

Oats, the fourth most important cereal crop of man, has been profoundly affected by its association with man. Let us, therefore, turn our attention to this association in the hope of learning when, where and how it began and by what means it may have affected the evolution of oats. Archaeology, written history and the present agricultural practices of conservative peoples throw light on this aspect of the problem.

Archaeology

What are probably the oldest known oat grains were found in Egypt associated with remains belonging to the 12th Dynasty (Täckholm et al., 1941). Similar grains have been found among Egyptian cereals of the 2nd and 3rd century A.D. These Egyptian oats were originally identified as *A. strigosa*, but Täckholm et al. think they are *A. fatua* or *A. sterilis*. It would appear that they occurred as weeds, there being no evidence that oats were cultivated by the ancient Egyptians (De Candolle, 1883; Ames, 1939).

Archaeological evidence for the early presence of oats in northwestern Europe is abundant. Werth (1944) lists three sites in Switzerland, five in Germany and one in

Denmark in which *A. sativa* grains have been found for the period 2000–1000 B.C., and there is an unbroken series of finds for that species from 1000 B.C. to the present. *A. strigosa* also occurred in Europe during the Bronze Age, as grains of that species from one site in Switzerland and one in adjacent France have been identified by Mal'tsev (Jessen and Helbaek, 1944).

Oats appear to have reached Britain somewhat later, with the earliest samples of *A. strigosa* or *A. brevis* and *A. sativa* dated about 150 B.C. (Jessen and Helbaek, 1944). Early remains of oats from England are always found mixed with larger samples of wheat and barley, suggesting the oats were weeds. Samples from Scotland, however, are almost exclusively oats. Oat culture in Britain seems to have increased following the Anglo-Saxon invasions and *A. fatua* appears in grain samples from this period.

Written Records

The written history of oats begins with the Greeks and Romans. According to Stanton (1936), Theophrastus, Cato, Cicero, Ovid and Varro knew oats only as a weed which was sometimes used for medicinal purposes. Thus oats were not cultivated in the ancient world of those writers, and De Candolle (1883) reported that oat culture was not introduced to Greece and Italy until the latter half of the Roman Empire. However, Columella and Pliny (Werth, 1944) indicate that the German barbarians ate oatmeal, and De Candolle interpreted the remarks of Pliny to indicate the Romans were not acquainted with its use. Also Galen wrote (according to De Candolle) that oats abounded in parts of Asia Minor where they were fed to horses, but were also eaten by men in times of distress. Other records for the early culture of oats in the Near East are wanting. Moldenke and

Moldenke (1952) have found no reference to cultivated oats in the Bible; there is no evidence that oats were grown in ancient Mesopotamia, nor are they grown in that region today. In China, however, De Candolle reported that naked oats are first mentioned in a history treating the years 618 to 907 A.D.

Archaeology and history indicate that *A. strigosa* and *A. sativa* were cultivated in northern Europe from 2000 B.C. on. However, the evidence is very incomplete from the Near East where Vavilov placed the center of origin of hexaploid cultivated oats. The evidence does indicate that oats at first were weeds, especially of other cereals, and even today *A. sativa* ssp. *macrantha* is not cultivated as an independent crop. This brings us to another aspect of the problem.

Oats as Weeds

Vavilov (1926) reported collecting many samples of emmer wheat from the several scattered localities where that ancient crop is still grown. There were samples from the Basques of the Pyrenees, from Abyssinia, Bulgaria, Asia Minor, the Crimea, the Caucasus, Iran and parts of Russia. One hundred samples of emmer from these localities proved to have admixtures of some *Avena* species, many of them unique varieties. Vavilov came to speak of oats as the unfailing attendant of emmer and concluded the history of oats was intimately connected with that of emmer. He visualized emmer spreading over the Old World and carrying with it an assortment of oats as weeds. When they reached the harsher climates of the north, oats, being the hardier plant, supplanted emmer and became an independent crop. In this connection Werth (1944) stated that emmer with its attendant oats was a widespread crop in northern Europe during the time of the Climatic Optimum. When the climate

began to deteriorate (from about 2000 B.C. on, according to Werth), the oats were better adapted to the changed conditions and supplanted the emmer.

The existence of oats as weeds of other cereals undoubtedly has had a profound influence upon the evolution of the genus. In the first place any mutation in a wild weed-oat causing non-articulate florets would have a selective value, as those grains which did not fall would be harvested with the main crop and planted next year. Similar mutations arising in the wild would be lethal.

Some species of the genus, with man as an agent of dispersal, have spread far from their native homes. No doubt *A. strigosa* and *A. abyssinica* achieved geographic isolation in this way, while *A. sativa* and *A. fatua* have encircled the globe. These species have achieved vastly larger populations than they would have otherwise, and the survival of new mutants under differing ecological conditions must have added greatly to the total variability of the species. In addition, the dispersal of oats by man probably has brought together species which were once isolated geographically, thus facilitating hybridization. At present we can but dimly see how this process has added to the variability of *A. sterilis* and *A. fatua*, but perhaps it explains why *A. sterilis* ssp. *Ludoviciana* resembles *A. fatua*, within whose range it lies, while *A. fatua* ssp. *meridionalis* which lies within the range of *A. sterilis* has the largest spikelets of the *fatua* group.

Modern Oats

It is fitting to end this review with a tribute to the many oat breeders who, during the past half century, have dedicated themselves to the never-ending battle against parasitic fungi. It has been found that the primary sources of disease resistance in oats are *A. byzantina* and *A. sterilis* (Coffman, 1946), and oat-breeding projects

have been largely concerned with transferring this resistance to varieties of *A. sativa*. Stanton (1947) gave a graphic account of a portion of this work by tracing the history of a single seed which resulted from an *A. byzantina* × *A. sativa* cross made in 1930. The descendants of this seed proved superior to the oats then grown and it is estimated that in 1946 they accounted for two-thirds of the oat acreage in the United States. As pointed out by Coffman, cultivated oats will come to contain more and more genes of *A. byzantina* with the advance of oat-breeding projects. The days of pure *A. sativa* appear to be numbered and we can well imagine that a phylogenist of the future will be able to assemble an extensive series of intermediate forms which, if their true origin were ignored, would suggest *A. sativa* originated from the red oats.

CONCLUSION

Scarcely any definite conclusions, other than broad generalizations, can be drawn as to the origin of oats. Objections raise themselves to every theory. However, the broad outlines of oat evolution are becoming evident, and, with the accumulation of more information, a much more satisfactory picture will develop. A measure of the progress to date can be gained by comparing the evidence reviewed here with notions held during the eighteenth century when, according to De Candolle, the prevailing opinion was that oats originated in the South Pacific on the Isles of Juan Fernandez.

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ERRATA

- Page 2, line 8
for Schltr. read Schlechter
- Page 4, line 21
omit Beih.
- Page 5, line 27
for T read I
- Page 6, line 27
for Murayaco read Murayaca
- Page 65, line 2
for cretaceous read Cretaceous
- Page 65, line 13
for cambrian read Cambrian
- Page 68, line 24
for cretaceous read Cretaceous
- Page 69, line 6
for proterozoic read Proterozoic
- Page 137, line 2
for *tomato* read tomato
- Page 140, line 18
for **emarginatus** read **marginatus**
- Page 147, line 17
add *L.* after **S. Mombin**
- Page 153, line 16
for *emarginatus* read *marginatus*
- Page 153, line 36
for *viridis* read *viride*
- Page 156, line 2
for *cherimolia* read *Cherimolia*
- No. 8, Explanation of Plate XXX, line 4
for *Tetrapteria* read *Tetrapteris*
- No. 9, throughout
for Belles Artes read Bellas Artes
- No. 9, Table I, last column, line 5 (data for *Tripsacum latifolium*)
for 1:1.4 read 1:4.1

